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APPLIED ISSUE

Estimating the stocking potential of fish in impoundments by modelling supply and steady-state demand

JAMES A. SMITH[*,†], LEE J. BAUMGARTNER[‡], IAIN M. SUTHERS[*,†], MATTHEW C. IVES[§] AND MATTHEW D. TAYLOR[*,†,§]

[*]*Evolution and Ecology Research Centre, and School of Biological, Earth and Environmental Science, University of New South Wales, Sydney, NSW, Australia*

[†]*Sydney Institute of Marine Science, Mosman, NSW, Australia*

[‡]*Fisheries and Ecosystems Research, Narrandera Fisheries Centre, NSW Department of Primary Industries, Narrandera, NSW, Australia*

[§]*Wild Fisheries Research, NSW Department of Primary Industries, Cronulla, NSW, Australia*

SUMMARY

1. Fish stocking is an increasingly common management tool for freshwater and marine environments and is often used to create and maintain fisheries in closed waters. The densities at which fish are stocked can have a large impact on a stocking programme's success and sustainability. Stocking densities in impoundment sport-fisheries, for example, are often based on social or practical factors, and ecologically based stocking models are needed to assist the selection of stocking densities that are appropriate for the environment.
2. In this study, stocking density is calculated with a numerical model that balances the supply of prey production with the energetic demand of stocked fish. The model aims to deliver outcomes over a range of potential management objectives, by providing specific consumption scenarios that represent the trade-off between population abundance and individual body size in stocked fisheries.
3. The model uses a steady-state population approach to calculate stocking density, which optimises population consumption by maintaining a consistent biomass distribution and encourages sustainable stocking by considering the energetic needs of all cohorts. Carrying capacity is represented by the steady-state stocking density under a minimum consumption scenario (when fish meet only their minimum energetic needs). The comparison between a desired consumption rate and the existing level of production is used to assess the status or 'health' of the existing population and is used to determine whether stocking can occur and whether stocking densities can be sustainably increased. The probability of incorrectly assuming populations are achieving a given consumption level is also estimated, which is an ideal approach for interpreting multiple probability distributions.
4. A Monte-Carlo analysis of uncertainty was used to provide a probability distribution of stocking density of Australian bass (*Macquaria novemaculeata*) in three Australian impoundments under various seasonal and consumption scenarios. The likely consumption rates of the existing populations were determined using historical stocking densities, which showed that the three populations were of reasonable health, although one impoundment may be overstocked. The steady-state stocking densities depended on the desired consumption rate, and there was an eightfold difference in the stocking density aimed at providing large 'trophy' fish and the density required to reach carrying capacity.
5. Model outputs of existing abundance and biomass density agreed with empirical estimates of abundance and relative density in these impoundments, which provides support to the model's

Correspondence: James A. Smith, Evolution and Ecology Research Centre, and School of Biological, Earth and Environmental Science, University of New South Wales, Sydney 2052, NSW, Australia. E-mail: james.smith@unsw.edu.au

accuracy. This supply–demand approach to estimating the range of appropriate stocking densities shows promise as a decision-support tool for stocked impoundments and other closed fisheries.

Keywords: Australian bass, carrying capacity, consumption, production, stocking density

Introduction

Accurately estimating stocking density is crucial to the success of fish stocking for creating, enhancing and maintaining fisheries. Stocking fish at densities appropriate for a fishery's capacity is crucial if surplus prey production is to be fully exploited while avoiding severe losses because of density-dependent growth and mortality. This is particularly the case in closed systems such as impoundments, which are closed to the free exchange of fish with the downstream environment. Some existing population or stocking models estimate stocking density but focus only on the energetic needs of a particular life stage (Taylor & Suthers, 2008), or do not consider ecosystem production (Lorenzen, 1995, 2005). If appropriate stocking densities are to be predicted for specific impoundments, then a production-based approach that incorporates the unique qualities of closed fisheries is needed.

If it is assumed that impoundments are closed to the natural exchange of individuals, and that all life stages co-exist within the system, then a stocking model for impoundments needs to incorporate the energetic requirements of the entire population (i.e. from stocking till death) when determining stocking density. Furthermore, impoundment fisheries are often maintained by stocking, which highlights the need for sustainable stocking densities that consider the requirements of cohorts to be stocked in future years. This study uses a steady-state population model to estimate the needs of an impoundment's entire population. It calculates a steady-state stocking density, which represents the cohort that is most suitable for utilising impoundment production sustainably. The application of the steady-state approach for calculating stocking densities is tested here.

Stocking densities in impoundments can be strongly influenced by particular management objectives. The stock structure of impoundment fisheries is often the direct result of a management strategy, particularly when natural recruitment is low or non-existent, which highlights the trade-off managers must make (deliberately or inadvertently) between creating a low-yield 'trophy' fishery or a high-yield fishery that maximises abundance (Walters & Post, 1993). This trade-off emphasises that what is 'optimal' for one fishery may be inappropriate for another based solely on differing management objectives. Incorporating this trade-off into the calculation of stocking densities also means that the carrying capacity concept, which is often mentioned in conjunction with stocking densities (Cowx, 1994; Blankenship & Leber, 1995; Munro & Bell, 1997), may be mostly a theoretical (and entirely unpractical) reference for maximum stocking densities rather than a realistic goal. The trade-off is conceptualised in this study using the consumption rate of individuals and how much they are compromised by the impoundment's management plan. This allows a range of stocking densities to be calculated, which encompass the particular goals for the most efficient population with the biggest fish, the most abundant fish, or a population that compromises between growth and abundance.

This article presents an impoundment stocking model that estimates stocking density by equalising the energetic demand of stocked cohorts with the impoundment-specific supply of available surplus productivity. It was used to approximate the status and stocking potential of three study impoundments in New South Wales, Australia (Fig. 1), for the Australian bass (*Macquaria novemaculeata* Steindachner, 1866). This study also proposes the use of a steady-state population model to effectively manage closed fisheries.

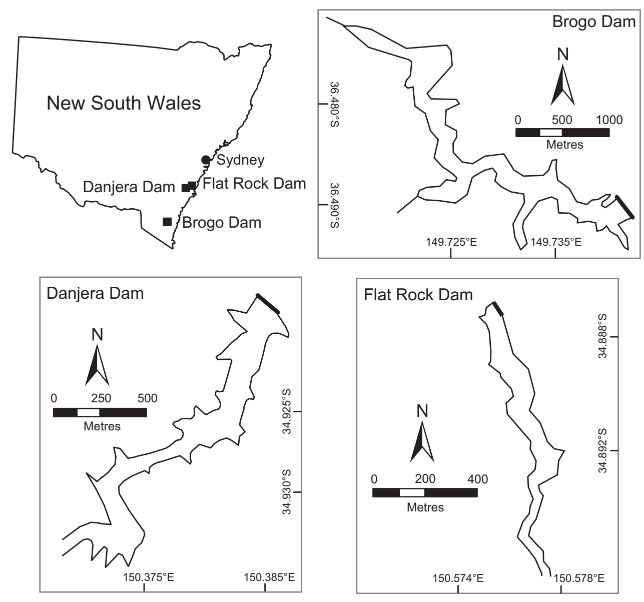

Fig. 1 Map of the three impoundments used to test the stocking model.

Model approach

General approach

This model combines basic population dynamics with production and habitat submodels to create a production-based single-species stocking model. Characteristics of stocked cohorts are determined by component models expressed as vectors over the life of each cohort, and the characteristics of the stocked population are derived from the characteristics of all the stocked cohorts combined. Stocking density is ultimately based upon the productive capacity of the impoundment. This can be considered a supply–demand approach, as the capacity of an impoundment for stocked fish is determined by matching the energetic requirements of stocked fish (demand) with the existing production of prey resources (supply) (Fig. 2). There are factors other than food which can determine the capacity of an environment for stocked fish (e.g. essential habitat types; Loneragan *et al.*, 2004), but a production model is justified in these impoundment fisheries for two reasons: (i) populations that are heavily stocked bypass the bottlenecks sometimes imposed by spawning or larval/fry refuge habitat and (ii) Australian bass are flexible users of habitat (Smith *et al.*, 2011a), so population size is unlikely to be limited by a particular habitat type. Habitat is incorporated in the model, but only as a determinant of food availability (Fig. 2).

Supply and demand can vary seasonally, which would alter the appropriate stocking density. The current model was run using values collected in summer and winter to

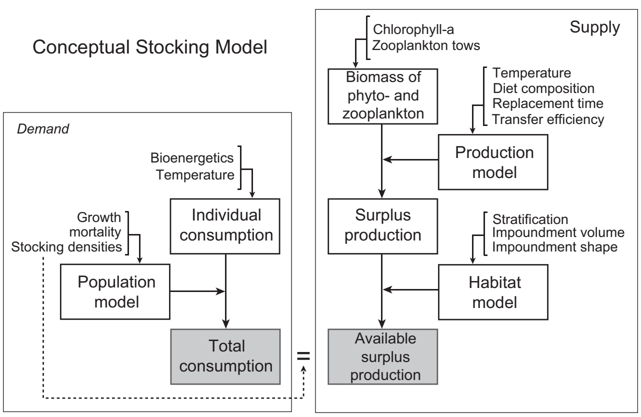

Fig. 2 The conceptual stocking model. Component models encompassing consumption, growth and mortality, production and distributional availability allow the calculation of the stocked population's total consumption and the impoundment's available surplus productivity. The model's aim is to determine the appropriate stocking densities that equalise total consumption (at a desired individual consumption level) with the available productivity (dotted arrow).

consider this variation. The management objectives (in terms of providing the biggest fish or the most fish) may vary between fisheries. This is expressed in the model in the consumption component, such that stocking densities are estimated based upon the extremes of consumption and a likely compromise (Fig. 3). The body mass–specific average (C_{av}), maximum (C_{max}) and minimum (C_{min}) consumption rates are estimated, which each provide a unique stocking density based on the corresponding population's demand. A fishery that aims to provide large trophy fish, for example, would use the stocking density estimated for the C_{max} scenario, which is much smaller than the stocking density calculated for the C_{av} and C_{min} scenarios. In this model, the stocking densities for the C_{min} scenario can be interpreted as those necessary to reach an impoundment's carrying capacity.

Model outputs

There are five main outputs from the model aimed at determining the appropriate stocking density (Fig. 3). Firstly, the model applies the population components to the stocking history to estimate the energetic demand of the current population under the three consumption scenarios, which are compared with the estimated production (Fig. 3 – box 1). This gives an idea as to the current status of the population prior to stocking, in terms of how much of their energetic demand is being achieved. The closer the peak of the C_{max} scenario is to the peak of available production, the more likely the population is to be maximising food intake. This information is used to determine how the impoundment should be stocked. If the status of the current population is deemed acceptable, then stocking densities are calculated to maintain the current consumption rate (Fig. 3 – box 2). If the existing population is deemed to be under-utilising the available production, then stocking densities are calculated that will increase the population's total consumption to match productivity (Fig. 3 – box 3). If the population is deemed to be overstocked, and the likely consumption rate is below the desired level, then the model will forecast the next 5 years to determine when stocking can resume under an improved consumption rate (Fig. 3 – box 4). Finally, stocking densities are calculated based on a hypothetical population that is in a steady state (discussed below), to create a reference for the maximum stocking densities for each consumption scenario and to calculate the carrying capacity (Fig. 3 – box 5).

All outputs rely on interpreting probability density functions (pdfs) resulting from model simulations. The uncertainty that exists within the environment and within

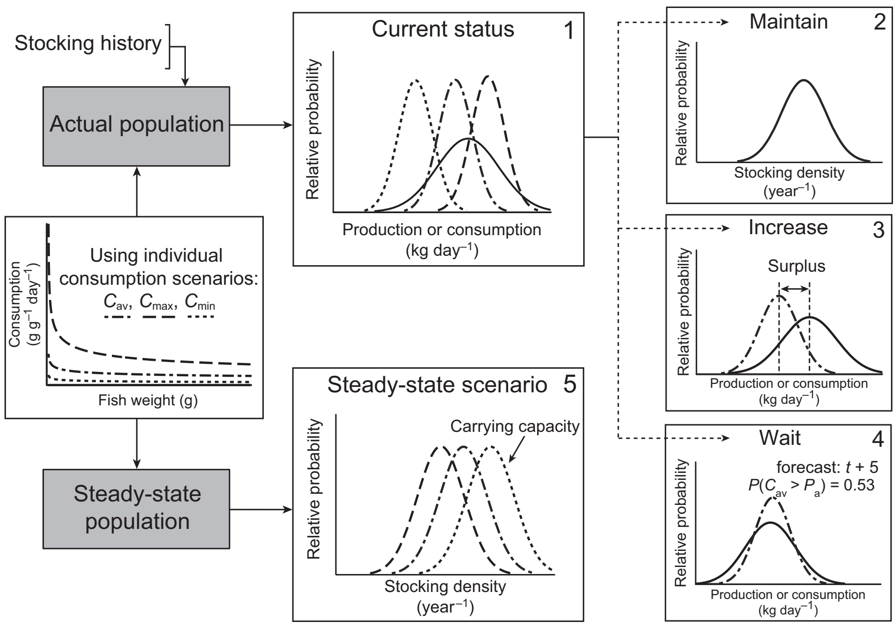

Fig. 3 The model's stocking density outputs. Three consumption scenarios are used as reference points in the model, indicating optimal health and growth (C_{max}, dashed line), average health and growth (C_{av}, dot-dashed line) and the minimum allowable health and growth (C_{min}, dotted line). These scenarios are used in conjunction with the stocking history to assess the status of the existing population (1) relative to production (unbroken line). This status is used to determine the appropriate stocking approach: to stock at densities that maintain the current population's total consumption level (2); to stock at densities that increase the population's consumption (3); or to post-pone stocking because of an unacceptable current consumption level, and instead forecast the duration to when stocking can resume (4). The consumption scenarios are also used to give reference stocking numbers that make the most efficient use of production, by assuming the stocked population is in a steady state (5). The stocking densities under the C_{min} scenario in this steady-state population are considered to be those that achieve carrying capacity.

the model can be significant, resulting in stocking density estimates with a wide confidence interval. The model attempts to ameliorate this by estimating the probability that a particular consumption scenario will exceed production (Fig. 4). The probability that the desired consumption rate (C_{av}, C_{max} or C_{min}) exceeds the available surplus productivity (P_a) is reported, for example $P(C_{\mathrm{av}} > P_a)$. This probability represents the proportion of individual model simulations in which the required consumption rate for the existing population was larger than the estimate of P_a. It is calculated as the proportion of the normal pdf of the $\log_{10}$-transformed ratio of $C : P_a$, which is greater than zero (Fig. 4), where C represents one of the three consumption scenarios. In this study, $P(C_{\mathrm{min}} > P_a)$ is interpreted as the probability that the modelled stocking regime will exceed carrying capacity (i.e. some of the stocked fish cannot possibly survive).

The steady-state population

The steady-state population model is useful for considering the energetic requirements of entire populations when calculating stocking density in closed systems [i.e. all life stages exist within the system, and population size is determined by recruitment (natural and/or stocking) and total mortality]. It represents the population in which every cohort behaves identically. This means that the component models which dictate the growth, mortality and consumption of one cohort also represent the steady-state population, for example the population's yearly consumption is equal to the lifetime consumption of a single cohort. The benefit of using the steady-state population to calculate the stocking density of a cohort is that the energetic needs of the entire population are simultaneously considered, as are the needs of future cohorts. The steady-state population and the trajectory of a steady-state cohort are identical, meaning that both can be defined by a mortality function (eqn 3). Integrating this function and the associated consumption calculations yields the total daily consumption (TDC) of the population (eqn 20). The mortality function includes the starting population size (N_0; eqn 3), and therefore, stocking density is simply calculated as the N_0 for the particular steady-state population that has a TDC equal to the available productivity (Fig. 2). This steady-state approach is the core concept of the stocking model.

The steady-state population model is used to estimate all stocking densities in the model, including those that

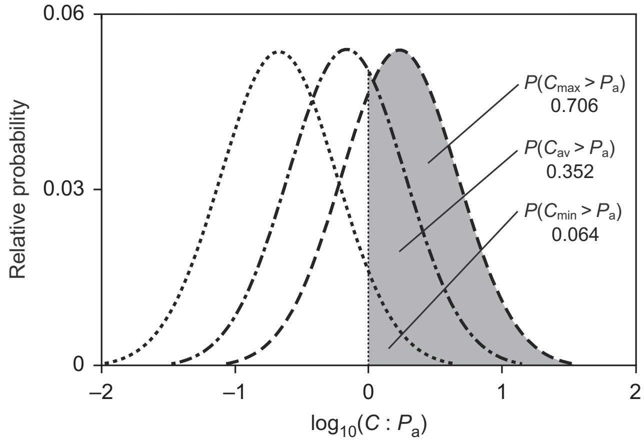

Fig. 4 Probability density functions (pdfs) of the $\log_{10}$-transformed ratio $C : P_a$ (where C represents the consumption scenarios C_{av}, C_{min} or C_{max}), generated from the 5000 model simulations. The proportion of a pdf which is greater than zero (in grey) represents the probability that the requirements of the actual population under a desired consumption scenario (C_{av}, dot-dashed line; C_{max}, dashed line; C_{min}, dotted line) exceed production. In this example, the probability that the actual population of fish is achieving less than their average consumption rate, $P(C_{av} > P_a)$, is 0.352.

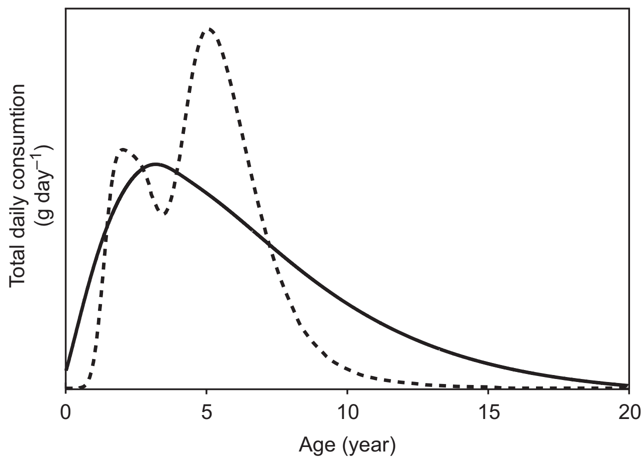

Fig. 5 A comparison of the steady-state total daily consumption (TDC) rate (TC_t; eqn 19) relationship (full line) and an actual TC_t relationship (dotted line; Brogo Dam 2010). The integrals of these curves are used to calculate the population's TDC (eqn 20). The steady-state TC_t also represents the trajectory of every steady-state cohort and does not change. The actual TDC relationship will vary in shape, mostly due to variation in stocking densities and stocking interval.

consider the existing population. The advantage of this approach remains in non-steady-state populations, that is, the needs of all cohorts are simultaneously considered. The only drawback in real populations is the possibility of an irregular stock structure (Fig. 5), which means that the steady-state stocking density for real populations will vary between stocking events in response to the changing TDC of a population. The model attempts to address this and aid decision making by forecasting the predicted consumption of the population (Fig. 3). The steady-state model is also an effective method of estimating carrying capacity. This is because carrying capacity is the maximum population biomass that can be achieved sustainably (Daily & Ehrlich, 1992), and the steady-state population is, by definition, sustainable.

Model structure

The model consolidates numerous component models to achieve its goals (Fig. 2). The values of the parameters and variables in the following equations used in model simulations are listed and their sources described in Tables 1 & 2.

Growth

The length–weight relationship was calculated for each impoundment according to

$$W_t = aL_t^b, \tag{1}$$

where W_t is mass and L_t is length at time t, and a and b are constants. Mass can be expressed as a function of time t (W_t) by substituting L_t in eqn 1 with the von Bertalanffy growth equation:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}), \tag{2}$$

where L_∞ is the asymptotic length (mm), k is the von Bertalanffy growth coefficient, and t_0 is the theoretical age at which $L_t = 0$.

Mortality

The number of fish alive at time t (N_t) is estimated as the product of the number stocked (N_0) and survivorship (S_t):

$$N_t = N_0 \times S_t \tag{3}$$

Survivorship (S_t) at time t is determined as the product of survivorship functions expressing the contributions of natural mortality (S_{M_t}) and fishing mortality (S_{F_t}):

$$S_t = S_{M_t} \times S_{F_t} \tag{4}$$

Survivorship after natural mortality (S_{M_t}) as a function of t is derived from the von Bertalanffy variant of the length-based survival equation by Lorenzen (2000):

Table 1 The parameter values used in model simulations for Brogo Dam (refer to specific equations for descriptions and units). Values in parentheses are the winter alternatives to the summer values of seasonally variable parameters. The uncertainty is given for those parameters varied within the model and represents the standard deviation of normal probability density functions. The parameters used in the sensitivity analysis are in bold. Parameter values were estimated from either data collected from the study impoundments, data derived from laboratory experiments, the cited literature, or are inferred (see text for details)

Parameter	Equation	Value	Uncertainty	Source
a	1	0.0000128825		Field data
b	1	3.021		Field data
$\boldsymbol{L_\infty}$	2	399.9	11.2*	Field data
$\boldsymbol{k}$	2	0.24	0.015*	Field data
t_0	2	−0.31		Field data
L_0	5	25		Pers. comm.†
$\boldsymbol{M_r}$	5	0.3	0.03	Field data (Appendix S1)
L_r	5	300		Field data (Appendix S1)
$\boldsymbol{F}$	6	0.1	0.02	Best guess (Appendix S1)
c	6	−15.674		Best guess (Appendix S1)
d	6	0.0627		Best guess (Appendix S1)
$\boldsymbol{T}$	7, 10, 11, 20, 21, 23, 24	20 (9.5)	2 (1)	Field data
A	7, 8	2.44		Field data
$\boldsymbol{\beta}$	9, 11	0.8		Experiment data
W_r	9	500		Inferred
$\boldsymbol{a_{\mathrm{max}}}$	10	0.112		Experiment data
$\boldsymbol{b_{\mathrm{max}}}$	10	−0.3		Stewart *et al.* (1983); Cyterski *et al.* (2002)
$\boldsymbol{q}$	10, 11	0.05		Best guess; Stewart *et al.* (1983)
$\boldsymbol{a_{\mathrm{min}}}$	11	0.008		Field data; inferred
Chla	12	7.48 (3.46)	1.87 (0.87)	Field data
$\boldsymbol{P_{\mathrm{Chla}}}$	12	0.0045	0.001	Literature (Appendix S2)
t_{pr}	13	2 days at 20 °C‡		Literature (Appendix S2)
$\boldsymbol{B_z}$	13	0.21 (0.14)	0.053 (0.035)	Field data
t_{zr}	13	3.47 days at 20 °C‡		Literature (Appendix S2)
V_{max}	15	8 980 000		Pers. comm.§
V_c	15	100		Field data
d_{max}	17	23		Pers. comm.§
d_h	17	9.6 (0)		Field data
$\boldsymbol{TE}$	18	0.1	0.05	Pauly & Christensen (1995)
$\boldsymbol{TL_b}$	18	3.43 (3.22)	0.18 (0.15)	Field data (Appendix S3)
TL_p	18	1		Pauly & Christensen (1995)
TL_z	18	2		Pauly & Christensen (1995)
$\boldsymbol{D_p}$	18	0.45 (0.33)	0.090 (0.066)	Field data (Appendix S3)
$\boldsymbol{D_z}$	18	0.49 (0.64)	0.098 (0.128)	Field data (Appendix S3)
$\boldsymbol{E}$	18	0.1		Inferred
t_{max}	20	20		Field data; Harris, (1985a)

*Errors estimated from outputs of variance–covariance matrix.
†Personal communication with the NSW Department of Primary Industries.
‡These values used to calculate eqns 23 & 24 (see Appendices).
§Personal communication with NSW Office of Water and Shoalhaven Council.

$$S_{M_t} = \left(\frac{L_0}{L_0 + L_\infty(e^{kt} - 1)}\right)^{\frac{M_r L_r}{L_\infty k}}, \quad (5)$$

where L_0 is the length of fish when stocked (mm), L_∞ and k are as described above, and M_r is the mortality rate at reference length L_r. Survivorship after fishing mortality (S_{F_t}) is determined by the product of instantaneous fishing mortality rate (F) and a length-based logistic selectivity curve:

$$S_{F_t} = e^{-F \times \frac{e^{(c+dL_t)}}{1+e^{(c+dL_t)}}}, \quad (6)$$

where c and d are constants and L_t is the length of a fish at time t. L_t is substituted with the von Bertalanffy growth equation to make S_{F_t} a function of t. The parameters c and d were selected to enable a L_{50} = 250 mm (the length for 50% retention) and a selection range of 35 mm (see Appendix S1). Natural recruitment is not considered in this model, because Australian bass are unable to spawn

Table 2 The parameter values used in model simulations for Danjera and Flat Rock Dams, which differ from the standard values used for all impoundments (Table 1). Values in parentheses are the winter alternatives to the summer values of seasonally variable parameters (refer to specific equations for descriptions and units). The uncertainty is given for those parameters varied within the model and represents the standard deviation of normal probability density functions for those parameters

		Danjera		Flat Rock	
Parameter	Equation	Value	Uncertainty	Value	Uncertainty
a	1	0.0000101859		0.0000169044	
b	1	3.064		2.973	
L_∞	2	352.8	12.6*	474.7	35.1*
k	2	0.270	0.027*	0.179	0.024*
t_0	2	−0.52		−0.1	
T	7, 10, 11, 20, 21, 23, 24	23 (11)	2 (1)	22 (10)	2 (1)
Chla	12	7.46 (1.66)	1.87 (0.42)	4.28 (4.13)	1.07 (1.03)
B_z	13	0.30 (0.16)	0.07 (0.04)	0.64 (1.42)	0.16 (0.36)
$V_{\max}$	15	7 800 000		400 000	
V_c	15	100		100	
$d_{\max}$	17	27		6	
d_h	17	20 (12)		4 (2)	

*Errors estimated from outputs of variance–covariance matrix.

in freshwaters (Harris, 1986). 'Recruitment' in this study is therefore only considered as densities stocked. Natural recruitment could be incorporated using a stock-recruitment model (Hilborn & Walters, 1992) and does not affect the steady-state approach.

Consumption

Three consumption levels are used to estimate stocking densities under various resource scenarios: maximum consumption ($C_{\max}$), minimum consumption ($C_{\min}$) and the likely average consumption (C_{av}). These are all in units of wet weight food per wet weight consumer (g g^{-1} day^{-1}). The average and minimum consumption rates were estimated using a power curve of weight (W) with the exponent determined by metabolic scaling coefficient (β). Metabolism (M) is known to be proportional to weight (W), such that $M \propto W^{\beta}$ (Bohlin *et al.*, 1994). If consumption (C; g) scales in proportion with metabolism, then $C \propto W^{\beta}$. Relative consumption (C_r; g g^{-1}) thus becomes $C_r \propto W^{\beta-1}$. This power curve determines the shape of the C_{av} and $C_{\min}$ relationships, with β equal to 0.8 (calculated from a feeding experiment; J. Smith, unpubl. data). The magnitude of the C_{av} function is determined using the relative consumption (C_r) regression of Palomares & Pauly (1998):

$$C_r = \frac{10^{7.964-0.204\log W_\infty-1.965T'+0.083A}}{365}, \tag{7}$$

where C_r is the relative consumption (g g^{-1} day^{-1}), W_∞ is the asymptotic weight of the population, T' is the temperature (T) of the waterbody in Kelvin units expressed as $T' = 1000\ (T + 273.15)^{-1}$, and A is caudal aspect ratio of the species, given by

$$A = \frac{h^2}{\text{SA}}, \tag{8}$$

where h is the height of the caudal fin and SA is its surface area. Relative consumption (C_r) is used to estimate the relative average consumption (C_{av}) of an adult Australian bass at a given reference weight (W_r), which is used in a relationship of average consumption as a function of weight (W) according to metabolic scaling:

$$C_{\text{av}} = \frac{C_r}{W_r^{\beta-1}} \times W^{\beta-1} \tag{9}$$

The maximum relative consumption ($C_{\max}$, g g^{-1} day^{-1} wet weight) is determined by a negative power curve of weight and an exponential function of temperature (Elliott, 1976):

$$C_{\max} = a_{\max} W^{b_{\max}} \times e^{qT}, \tag{10}$$

where $a_{\max}$, $b_{\max}$ and q are constants and T is temperature (°C). The value of $b_{\max}$ was estimated from studies on similar-sized fish (Stewart *et al.*, 1983; Cyterski, Ney & Duval, 2002), and the value of $a_{\max}$ was derived from a satiation feeding experiment using young captive Australian bass (J. Smith, unpubl. data). The minimum relative consumption ($C_{\min}$, g g^{-1} day^{-1} wet weight) necessary to meet the energetic demand of an Australian bass was calculated using a negative power curve of weight-at-age according to metabolic scaling, and an exponential function of temperature:

$$C_{\min} = a_{\min} W^{\beta-1} \times e^{qT}, \tag{11}$$

where $a_{\min}$ is a constant and β, q and T are as described above. The value of $a_{\min}$ was derived from a stomach-content analysis of adult Australian bass (>500 g), by assuming that the average wet weight of food in the stomach (g g^{-1}) represented the minimum daily consumption at that temperature. The constant q was estimated by using a conservative estimate of that in the study by Stewart *et al.* (1983), which agreed with field and experimental data for maximum and minimum consumption rates. The three consumption curves C_{av}, $C_{\max}$ and $C_{\min}$ are illustrated in Fig. 3. Consumption as a function of age (e.g. C_{avt}) is calculated by substituting W (eqns 9, 10 & 11) with W_t (eqns 1 & 2).

Production

Phytoplankton production and zooplankton production are calculated by converting standing stock biomass into surplus productivity. Phytoplankton biomass is estimated from chlorophyll concentration using

$$B_p = \frac{\text{Chla}}{P_{\text{Chla}} \times 1000}, \tag{12}$$

where B_p is the biomass of phytoplankton (g m^{-3}), Chla is the concentration of chlorophyll-a (μg L^{-1}), and P_{Chla} is the proportion (by fresh weight) of phytoplankton made up by chlorophyll-a. This standing stock is converted to a surplus productivity (i.e. the biomass that can be sustainably harvested daily), using the average replacement time of the phytoplankton community:

$$P_p = \frac{B_p}{t_{pr}}, \tag{13}$$

where P_p is the surplus productivity of phytoplankton (g m^{-3} day^{-1}) and t_{pr} is the time (days) the phytoplankton population theoretically takes to double (or replace itself) in terms of biomass. This is a simple alternative to the common method of estimating P : B ratios (Ney, 1990) and is suited to prey species for which a replacement time makes biological sense (i.e. those with short generation times or that reproduce through cell division). The same method is used to estimate surplus zooplankton productivity (P_z; g m^{-3} day^{-1}) using direct field estimates of the standing stock biomass of zooplankton (B_z; g m^{-3}) and the replacement time for the zooplankton community (t_{zr}; days). Details of phytoplankton and zooplankton sampling and the estimation of P_{Chla}, t_{pr} and t_{zr} are given in Appendix S2.

The amount of production available can be dependent on the overlap between the distributions of predator and prey (Ney, 1990). This is an important consideration in closed waters because annual periods of stratification can alter the distribution of stocked fish (Smith *et al.*, 2011a) and partially segregate predator and prey (Cyterski & Ney, 2005). This was considered in the current model by allocating the productivity which occurred only in the habitat volume that was available to Australian bass (V_a; m^{-3}) to a stocked cohort. For example, the surplus-phytoplankton production that is available (P_{ap}; g day^{-1}) to Australian bass is calculated:

$$P_{ap} = P_p \times V_a \tag{14}$$

The same calculation is used to estimate the available surplus production of zooplankton (P_{az}). The available habitat volume in impoundments varies mostly because of changes in absolute volume and because of the isolation of bottom areas owing to stratification-driven hypoxia (Smith *et al.*, 2011a). Habitat availability is thus calculated:

$$V_a = V_{\max} \times \frac{V_c}{100} - V_{\max} \times \frac{V_u}{100}, \tag{15}$$

where V_a is as defined above, $V_{\max}$ is the volume of the impoundment when full (m^3), V_c is the current absolute volume (%), and V_u is the volume unavailable because of bottom hypoxia (%). V_c is a metric commonly recorded by the organisations that manage impoundments, but V_u requires a relationship between depth (d) and impoundment volume (V). The current model uses a three-segment linear function constructed using data from a study impoundment (Brogo Dam; NSW Office of Water, pers. comm.) and is the shape used for all study impoundments:

$$V = \begin{cases} 100 - \frac{6.1}{3}d\,, 0 \le d \le 30 \\ 72.75 - 1.125d\,, 30 < d \le 55\,, \\ \frac{80-0.8d}{3}\,, 55 < d \le 100 \end{cases} \tag{16}$$

where V is the impoundment volume (%) and d is the depth from the surface (% of maximum depth). This is used to calculate the volume made unavailable by bottom hypoxia (V_u; eqn 15), by calculating d as the depth from the surface (%) at which a threshold level of hypoxia begins, which is 4 mg L^{-1} dissolved oxygen for Australian bass (Smith *et al.*, 2011a):

$$d = \frac{d_{\max} - d_h}{d_{\max}} \times 100, \tag{17}$$

where $d_{\max}$ is the maximum depth (m) of the impoundment when full and d_h is the vertical distance (m) between the maximum depth and the depth at which the threshold level of hypoxia begins.

The amount of the available surplus production of phytoplankton (P_{ap}) that makes it through the food web to Australian bass is estimated using a general trophic transfer function (Pauly & Christensen, 1995). This is modified to include additional trophic variables to calculate the total amount of production available in a specific impoundment:

$$P_t = \frac{P_{ap} \times TE^{(TL_b - TL_p)}}{D_p} \times (1 - E), \tag{18}$$

where P_t is the total amount of production (g day^{-1}) that is directly available to Australian bass, TE is the trophic transfer efficiency, TL_b is the trophic level of Australian bass, TL_p is the trophic level of phytoplankton, D_p is the proportion of the diet of Australian bass that ultimately derives from phytoplankton, and E is the proportion of energy in the system dedicated to other consumers that share prey with Australian bass but are not prey of Australian bass themselves. This parameter would most often represent the biomass of direct competitors (such as other stocked percichthyids). Total productivity (P_t) is also calculated using estimates of zooplankton production, by substituting P_{az}, TL_z and D_z for the phytoplankton variables. These two estimates of P_t (one derived from phytoplankton and one from zooplankton) are averaged in the model to give a more robust estimate of P_t. The parameter D_p (or D_z) is a necessary addition, as it is often the case that 50% or more of the energy supporting impoundment fisheries is from allochthonous sources (Appendix S3; Reynolds, 2008; Solomon *et al.*, 2008). The parameter E is used to consider the energetic needs of other predatory fish and can be assigned based on the suspected proportion of total biomass (of that trophic level) that is made up by the target species. In the current study, E is a small value, because all study impoundments contained few other large consumers.

Equalising consumption and production

The TDC (g day^{-1}) of a cohort at age t (TC_t) is calculated as the product of abundance (N_t) and body mass (W_t) at age t and the average daily consumption of an individual at that age (C_{avt}, for example):

$$TC_t = N_t \times W_t \times C_{\mathrm{av}_t} \tag{19}$$

This equation is used to estimate the total consumption of both the actual and steady-state populations. The only difference between the two populations is that N_t and W_t in the steady-state case are assumed to be in a steady state and thus represent the basic relationships established over the life of one cohort. In the actual population, these relationships are more complicated and are the result of variable stocking events (i.e. a non-steady-state; Fig. 5). In the steady-state population, the integral of TC_t represents the total consumption of the population over its lifetime ($t_{\max}$, y), or the total yearly consumption of $t_{\max}$ cohorts (i.e. the yearly intake of the steady-state population). Dividing TC_t by 365 days provides an instantaneous estimate of the total daily consumption (TDC; g day^{-1}) of the steady-state population:

$$\mathrm{TDC} = \frac{\int_{t_0}^{t_{\max}} TC_t \, dt}{365}, \tag{20}$$

where $t_{\max}$ is the oldest age of a cohort and t_0 is the age at stocking. This approach is also used to estimate TDC for the actual population, but because of the non-steady-state stock structure, TDC is estimated for a particular day after stocking that coincided with the summer and winter seasons (summer: 30 days after stocking; winter: 200 days after stocking). The TDC calculated for each consumption scenario (C_{av}, $C_{\max}$, $C_{\min}$) is then used to estimate stocking density, by finding the steady-state population in terms of N_0 (eqn 3) which has a TDC equal to the available productivity (P_t). The steady-state population curve has N_0 proportional to the magnitude of its integration, which means that the steady-state stocking density (N_{0i}) can be calculated by finding the TDC (using eqn 20) of a reference population (TDC$_r$) that has a pre-determined starting population size (N_{0r}) and scaling this to P_t to find the stocking density:

$$N_{0_i} = \frac{P_t}{TDC_r} \times N_{0_r} \tag{21}$$

N_{0r} can be any value (10 000 in the current study). This equation is used to calculate the steady-state stocking densities (Fig. 3 – box 5), and P_t is replaced with the current population's TDC to calculate the 'maintain' stocking density (Fig. 3 – box 2).

Stocking densities can be estimated which increase the current consumption level, which is deemed to occur when production exceeds the requirements of the desired consumption level (i.e. a production surplus; Fig. 3 – box 3). Stocking density is then calculated as that needed to maintain consumption, plus that needed to create a steady-state population which has a TDC equal to this additional surplus production (P_t). This value approaches the steady-state stocking density (Fig. 3 – box 5), but is usually less, probably due to artefacts of the log-normal distributions.

Sensitivity analysis

A sensitivity analysis was carried out on parameters and variables likely to vary biologically and those with uncertain values, to determine the relative effect of these parameters in determining model outputs (Table 1). Monte-Carlo simulations were used to produce random sets of parameter values, consisting of either the assigned value or the value ± 10%. Simulations were continued until the variance in the steady-state stocking density stabilised (5000 simulations).

Parameter values were standardised according to the method of Kleijnen (1997), to determine the relative importance of parameters on the model output. Stepwise regression analysis was used to determine the best-fit equation of parameter values to the model output, as evaluated using Akaike's Information Criteria in the statistical package R (version 2.13.1, R development core team, http://www.R-project.org). The best model consisted of 10 parameters, which explained 75% of the variation in stocking density ($F = 341.1$, $P < 0.001$). The trophic level of bass (TL_b) and the population asymptotic length (L_∞) had the largest (and inverse) influence on stocking density (Fig. 6).

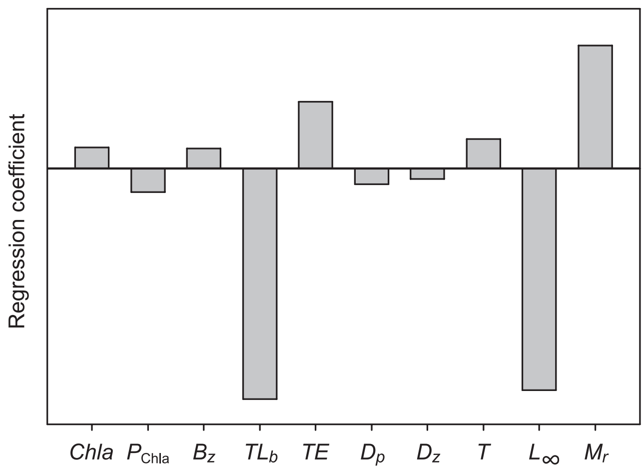

Fig. 6 Results of the sensitivity analysis. The bars represent the coefficients of the stepwise linear regression of standardised model parameters, which signifies the relative influence of key parameters on the model's steady-state stocking density output. The direction of the bars indicates whether a change in the parameter causes a similar change (above the *x*-axis) or inverse change (below the *x*-axis) in the stocking density output. Chla, concentration of chlorophyll-a; P_{Chla}, proportion of phytoplankton that is chlorophyll-a by mass; B_z, concentration of zooplankton; TL_b, trophic level of Australian bass; *TE*, trophic transfer efficiency; D_p, proportion of the Australian bass' diet derived from phytoplankton; D_z, proportion derived from zooplankton; *T*, average water temperature; L_∞, the population's asymptotic length; M_r, the natural mortality rate.

The 10 parameters from the sensitivity analysis were selected to be expressed in the model as probability density functions (Table 1). Uncertainty was expressed using a normal distribution, which had standard deviations that were estimated from data or were inferred. The correlation between the von Bertalanffy parameters k and L_∞ (eqn 2) was acknowledged in the model by assigning these parameters a multivariate probability density function. This was determined by the variance–covariance structure of these parameters during the nonlinear estimation of von Bertalanffy parameters.

Model simulations

All simulations were run in MATLAB v. R2010a (Mathworks, Natick, MA, U.S.A.). Definite integrals of consumption functions (eqn 20) were estimated in MATLAB using recursive adaptive Simpson quadrature. The model was designed as a Monte-Carlo analysis, with each model simulation sampling a value for varied parameters from their assigned probability density functions. Simulations continued until the variance in the steady-state stocking density for the C_{av} consumption scenario stabilised (5000 simulations). Probability density functions were created for most model outputs. Results represent the state of each fishery in the Australian summer 2010/2011 and winter 2011.

Study impoundments

Three impoundments stocked with Australian bass were selected to test the application of the stocking model: Brogo Dam (36.492°S, 149.740°E), Danjera Dam (34.920°S, 150.385°E) and Flat Rock Dam (34.888°S, 150.575°E) (Fig. 1). These are relatively small impoundments (Tables 1 & 2) stocked regularly with Australian bass (Appendix S5), with no other species stocked in recent years. Brogo and Danjera are similar in volume and depth, with similar undeveloped catchments, and are considered as being between oligotrophic and mesotrophic, based on their chlorophyll-a concentrations (Marshall & Peters, 1989). Flat Rock is much smaller and shallower with a more developed catchment and is approaching eutrophy, based on its catchment and occasional macrophyte blooms. Stock analysis and field sampling were carried out in each impoundment to parameterise the model (Tables 1 & 2; see Appendices). The current model assumes that impoundments are closed systems. Immigration is not possible in these study impoundments because there are no fishways. Emigration is occasionally possible during peaks in volume when the spillway is active, but these losses are assumed to be incorporated within total mortality (Appendix S1).

Results

The steady-state stocking densities that exploit the available surplus productivity (according to the three consumption scenarios) showed a large amount of variation between impoundments, seasons and consumption scenarios (Table 3). Log_{10}-normal distributions were used to define the model simulations. In Brogo Dam, average steady-state stocking densities ranged from 8472 to 68 707 fish per year in summer and 3864 to 31 117 in winter (Table 3; $N = 10^{\log_{10} N}$). These stocking densities scale linearly with stocking interval, meaning that the annual steady-state stocking density of 21 727 (C_{av}, summer) is equivalent to 43 454 stocked every 2 years. The 99% confidence intervals for most stocking densities encompassed approximately two orders of magnitude.

Carrying capacity in this model is represented by the steady-state stocking density for the C_{min} scenario. This was usually about three times greater than the C_{av} estimates, and about eight times greater than the C_{max} estimates, which the model gives as the target for creating a trophy fishery. The densities required to maintain the current population consumption ('maintain'; Fig. 3 – box 4) approximated a normal distribution and had much less uncertainty than other model outputs. The normal probability density functions (with mean μ and standard deviation σ) representing the annual maintenance stocking densities are as follows: Brogo Dam μ = 15 010; σ = 346.4; Danjera Dam μ = 10 133; σ = 172.7; and Flat Rock Dam μ = 2869; σ = 221.4.

The status of each population according to realised consumption is observed by incorporating production (Fig. 3 – box 1). In all impoundments, average production was likely to be insufficient to meet the TDC of the existing populations under the C_{max} scenario, with the probability (P) of this varying between 0.642 and 0.970 (Table 4). The consumption rate under the C_{av} scenario exceeded average production with $P > 0.5$ in Brogo Dam in winter for at least the following 2 years (Fig. 7, Table 4); Danjera Dam in winter of the modelled year, but with $P < 0.5$ in the following year (Table 4); Flat Rock Dam in summer for at least the next 5 years and in winter for at least the next 2 years (Table 4). The status of the populations (i.e. the likely actual consumption rate) was poorer in winter for Brogo and Danjera Dams, but improved in Flat Rock Dam in winter. This is because production did not decrease in Flat Rock as quickly as consumption rate, meaning that fish in winter had a greater relative energy intake than in summer. The probability that the modelled stocking regime would reach carrying capacity [$P(C_{min} > P_a)$] ranged from 0.041 in Danjera in summer to 0.355 in Flat Rock in summer (Table 4). Overall, the population in Danjera Dam likely has the best status, with an average $P(C_{av} > P_a) = 0.433$. This was followed by Brogo Dam (0.494), then Flat Rock Dam (0.682).

The average production (P_a) occasionally surpassed the modelled TDC for the actual population in the study

Table 4 Probabilities (P) that the total daily consumption of the existing populations under various consumption scenarios exceeds available production (P_a), as modelled using summer and winter parameter values. Average (C_{av}), maximum (C_{max}) and minimum consumption (C_{min}) scenarios are used for the current year (t) and for C_{av} forecasted up to 5 years (t + 5) without stocking. The calculation of these probabilities is illustrated in Fig. 4. In this study, $P(C_{min} > P_a)$ is interpreted as the probability that the modelled stocking regime will exceed (i.e. reach) carrying capacity

	Brogo		Danjera		Flat Rock	
	Summer	Winter	Summer	Winter	Summer	Winter
$P(C_{av} > P_a)$ (t)	0.352	0.635	0.307	0.558	0.777	0.586
$P(C_{max} > P_a)$ (t)	0.706	0.915	0.642	0.872	0.970	0.923
$P(C_{min} > P_a)$ (t)	0.064	0.208	0.041	0.122	0.355	0.176
$P(C_{av} > P_a)$ $(t + 1)$	0.327	0.596	0.264	0.491	0.762	0.560
$P(C_{av} > P_a)$ $(t + 2)$	0.291	0.544	0.217	0.415	0.734	0.522
$P(C_{av} > P_a)$ $(t + 5)$	0.166	0.350	0.094	0.201	0.598	0.370

Table 3 Means (μ) and standard deviations (σ) of the annual steady-state stocking density (N_{0i}), $\log_{10}$-normal distributions under the average (C_{av}), maximum (C_{max}) and minimum consumption (C_{min}) scenarios, using summer and winter values

	Brogo summer		Brogo winter		Danjera summer		Danjera winter		Flat Rock summer		Flat Rock winter	
	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ
N_{0i} C_{av}	4.337	0.438	4.016	0.409	4.196	0.424	3.897	0.382	3.160	0.411	3.379	0.387
N_{0i} C_{max}	3.928	0.434	3.587	0.405	3.806	0.419	3.487	0.377	2.721	0.405	2.919	0.380
N_{0i} C_{min}	4.837	0.437	4.493	0.410	4.728	0.423	4.410	0.381	3.615	0.410	3.813	0.386

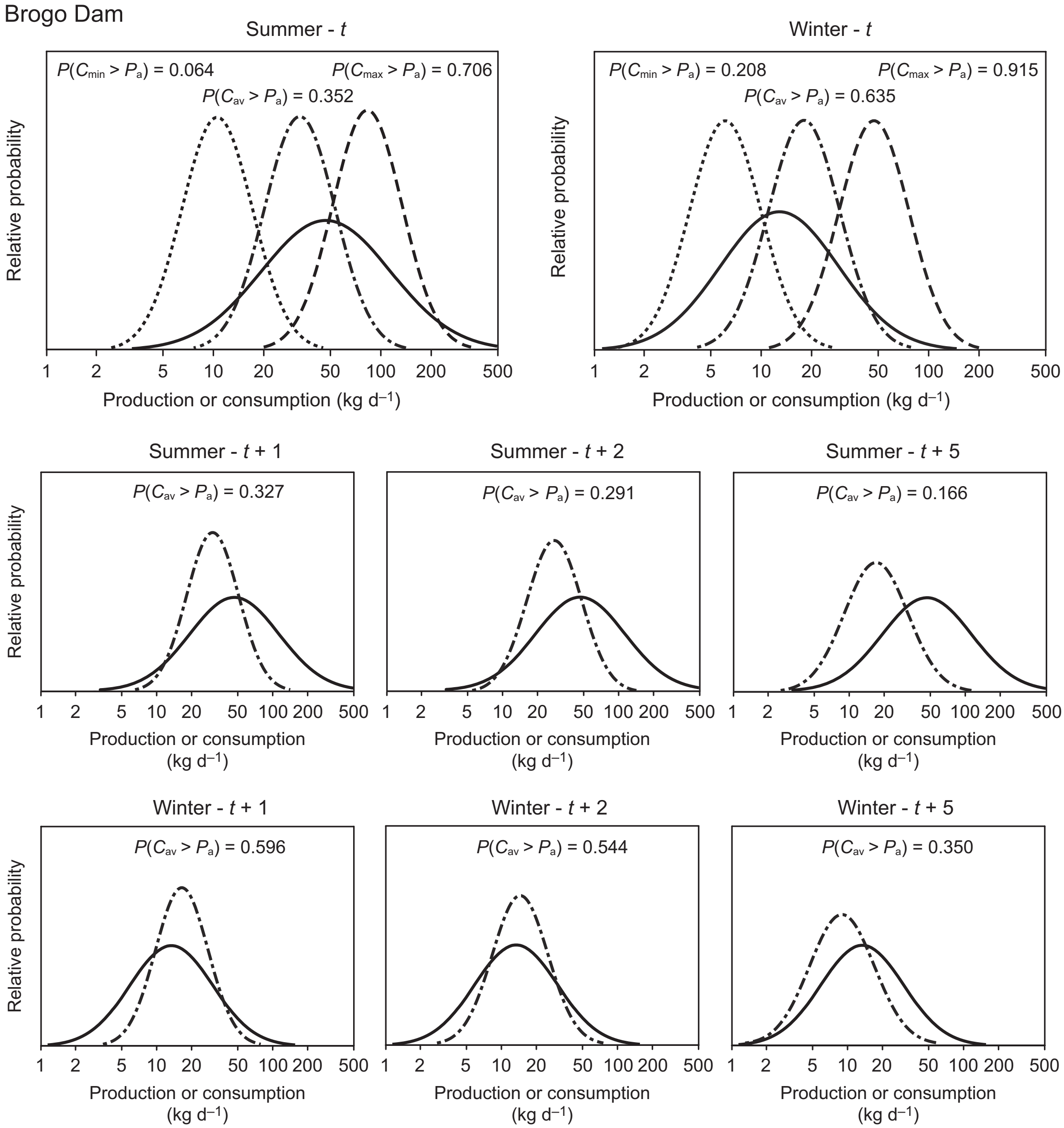

Fig. 7 Comparisons of production (P_a, unbroken line) and the resources required for the existing population in Brogo Dam under maximum (C_{max}, dashed line), average (C_{av}, dot-dashed line); and minimum consumption (C_{min}, dotted line) scenarios using summer 2010/2011 and winter 2011 values (time *t*). P_a and C_{av} requirements are forecasted for both seasons if stocking was postponed 1 year (t + 1), 2 years (t + 2) and 5 years (t + 5). Given is the probability (*P*) that the requirements of the actual population for the C_{av} scenario would exceed production ($C_{av} > P_a$). The *x*-axis is in $\log_{10}$ units.

impoundments (Table 5). This indicates the possibility for TDC to increase (Fig. 3 – box 3), which means that stocking numbers can be increased for a given consumption scenario. This 'surplus' production was allocated to a steady-state cohort (Table 6), and these additional stocking densities can be added to the maintenance stocking densities to calculate the overall annual stocking density.

The historical stocking densities indicate that Flat Rock Dam should have the poorest status, as the relative stocking densities have been two times to six times greater in this impoundment than Brogo or Danjera (Table 7). Despite this, the model predicts that carrying capacity in Flat Rock has still not been reached, and the impoundment is at 68% carrying capacity by biomass. The relative values of the catch per unit effort (CPUE) of Australian bass using gillnetting in the three impoundments (g 10 m^{-2} h^{-1}; Table 7) resemble the model's estimates for current biomass density (g m^{-3} V_a; Table 7).

Table 5 Mean (μ) and standard deviation (σ) of the available production (P_a) or actual total daily consumption $\log_{10}$-normal distributions for all three impoundments using summer and winter parameter values. Average, maximum and minimum consumption scenarios were simulated for the current year (t) and forecasted under the average scenario up to 5 years (t + 5) without stocking. The values for Brogo Dam are illustrated in Fig. 7. Units are $\log_{10}$(kg day^{-1})

	Brogo summer		Brogo winter		Danjera summer		Danjera winter		Flat Rock summer		Flat Rock winter	
	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ
P_a	1.678	0.386	1.114	0.356	1.539	0.377	0.980	0.324	0.453	0.337	0.391	0.298
TDC_{av} (t)	1.511	0.222	1.256	0.214	1.323	0.226	1.038	0.229	0.760	0.233	0.473	0.238
TDC_{max}	1.914	0.215	1.673	0.210	1.695	0.220	1.423	0.224	1.198	0.225	0.927	0.231
TDC_{min}	1.014	0.220	0.780	0.214	0.791	0.224	0.524	0.227	0.304	0.229	0.038	0.235
TDC_{av} (t + 1)	1.480	0.233	1.216	0.227	1.264	0.239	0.971	0.243	0.744	0.244	0.450	0.250
TDC_{av} (t + 2)	1.430	0.245	1.160	0.239	1.191	0.253	0.893	0.257	0.712	0.255	0.412	0.261
TDC_{av} (t + 3)	1.369	0.257	1.094	0.252	1.108	0.266	0.806	0.271	0.669	0.267	0.365	0.273
TDC_{av} (t + 4)	1.299	0.269	1.021	0.265	1.018	0.281	0.713	0.285	0.618	0.278	0.311	0.285
TDC_{av} (t + 5)	1.222	0.281	0.942	0.278	0.923	0.295	0.615	0.299	0.561	0.289	0.251	0.296

Table 6 The additional stocking densities (impoundment^{-1} year^{-1}) needed to increase the current population's consumption to the average (C_{av}), maximum (C_{max}) or minimum (C_{min}) rates that equalise the estimated surplus productivity (Fig. 3 – box 3). These are added to the average 'maintain' stocking densities to estimate each impoundment's total stocking density. These are forecasted to measure the increase in 'surplus' production over time (t). The values differ between impoundments and seasons, because of differences in production, habitat availability and population structure

	Brogo		Danjera		Flat Rock	
	Summer	Winter	Summer	Winter	Summer	Winter
C_{av} (t)	4720	0	3479	0	0	0
C_{max}	0	0	0	0	0	0
C_{min}	36 421	12 573	24 827	12 693	3636	9735
C_{av} (t + 1)	5433	0	4158	125	0	0
C_{av} (t + 2)	6440	0	4883	1122	0	0
C_{av} (t + 5)	9633	2546	6717	3509	0	1780

Discussion

This study compiles existing component models and introduces some novel and important aspects to create a comprehensive stocking model for closed systems. It makes progress for the improved management of stocked impoundments and lakes by acknowledging the variability that can exist in stocking densities owing to variation in seasonal factors, habitat availability and desired or expected consumption rate. The use of consumption scenarios to customise stocking densities to a particular impoundment's objectives should encourage a more flexible and transparent approach to calculating stocking densities.

The steady-state population model is a novel approach for predicting stocking densities. Incorporating the integral of steady-state populations (Miranda, 2002) and consumption relationships (Essington, Kitchell & Walters, 2001) into population dynamics is not new, but its use here as a reference and steady-state stocking density is novel. The assumption of a steady-state population that is maintained by stocking encourages sustainable stocking densities and is powerful in situations where the actual population is not well studied. Theoretically, the actual population size need not even be estimated to use

Table 7 Historical average stocking densities (N_0) and various model outputs representing the status of the studied impoundment fisheries: the volume of available habitat (V_a), the modelled population abundance (N), population biomass (B) and carrying capacities (CC; this is the steady-state population in the C_{min} scenario). V_a, N, B and CC are as modelled for January 2011. B and CC are calculated as total kg per impoundment (imp) and as g m^{-3} of available habitat. The actual catch per unit effort (CPUE) of fish caught with gillnets in 2010 is given as the catch rate by number (# 10 m^{-2} h^{-1}) and by mass (g 10 m^{-2} h^{-1})

Parameter	Units	Brogo	Danjera	Flat Rock
N_0	imp^{-1}	20 742	16 590	4873
N_0	m^{-2}; m^{-3}	0.021; 0.002	0.018; 0.002	0.046; 0.012
V_a	m^3	7 980 500	4 111 900	259 000
N	imp^{-1}	6456	3524	1033
B	kg imp^{-1}; g m^{-3} V_a	1556; 0.195	798; 0.194	272; 1.050
CC	kg imp^{-1}; g m^{-3} V_a	6934; 0.869	4188; 1.019	398; 1.537
CPUE	# 10 m^{-2} h^{-1}; g 10 m^{-2} h^{-1}	0.84; 236	0.69; 215	1.21; 350

steady-state stocking densities. If it is assumed that the actual population is small and underutilising the food resource (as opposed to estimating the current stock status; Fig. 3 – box 1), then stocking can commence using steady-state stocking densities modelled using site-specific production and habitat information and average parameter values for the stocked species. The complete model, however, would be most beneficial to those species for which model parameters are derived from empirical data.

This model also quantifies carrying capacity, which is a feature often noted as crucial to stocking management (Cowx, 1994; Blankenship & Leber, 1995; Munro & Bell, 1997) but usually absent from stocking models. In this study, carrying capacity is assumed to be the point at which the average individual in a population is meeting its minimum energetic requirements. It is unclear whether this situation represents the carrying capacity of wild populations, or is achievable in stocked fisheries without significantly increasing mortality rates (which would increase the stocking density required). In any case, the C_{min} scenario makes a useful upper limit for stocking densities. The model also makes useful relative comparisons regarding the carrying capacity; for example, it predicts that the stocking densities that ensure the average individual is achieving maximum consumption (C_{max}) are around eight times smaller than those needed to reach carrying capacity (C_{min}).

To stock or not

The status of a fishery is a main output of this model (Fig. 3 – box 1) and should be determined in stocked fisheries in which the existing population size can be accurately estimated. The current population consumption cannot exceed the available surplus production, and if a target consumption scenario does, then the actual consumption rate must be lower than that scenario (e.g. C_{av}, Brogo Dam in winter; Fig. 7). Whether the results for Brogo Dam, for example, indicate that it should not be stocked until the average winter C_{av} drops below average production [approximately when $P(C_{av} > P_a) < 0.5$] is left to a stocking manager's discretion. The population in Brogo Dam is mostly healthy (Smith *et al.*, 2011a), so it may be that the increased consumption rate in summer is driving the overall health of the population. Further field studies examining the role of production minima and maxima on population regulation are needed before this can be determined. In any case, the forecasting functionality and the reporting of the probabilities relating to consumption rate are comprehensive aids to determining when stocking should occur.

The stocking magnitude and frequency of steady-state cohorts

This model will be most beneficial to a stocked fishery when cohorts are stocked regularly at the specified rate. This will ensure the most regular distribution of biomass in the population, according to the steady-state population. The duration of the interval between steady-state stocking events determines their magnitude, and stocking densities estimated using the steady-state population model scale linearly, for example the annual stocking density is doubled if stocking occurs every 2 years. If the stocking interval varies, however, then stocking densities should not necessarily be scaled with interval, as the larger stocking events reduce the allowable stocking densities if stocking at the shorter interval resumes. This difference in stocking densities is not large, but will be more significant the larger the disparity between stocking intervals. The aim therefore should be to stock consistently according to the minimum expected stocking interval for the most evenly distributed population biomass in the long term. Regular stocking events have the added advantage of creating a more stable food web, particularly the zooplankton–phytoplankton size structure (Carpenter, Kitchell & Hodgson, 1985).

The limitation of applying the steady-state model in real-world scenarios is that all populations will have changing stock structures to some degree. This does not mean that the steady-state population approach cannot be used. It remains a powerful approach for considering the needs of all cohorts and for maintaining a reasonably stable distribution of biomass in real populations. The drawback is that the TDC in actual populations can increase between years as abundant cohorts age. This means that the steady-state stocking density in a given year may overestimate future steady-state stocking densities. If the model is used annually, however, and use is made of the forecasting output (Fig. 3 – box 4), serious overstocking will be avoided.

Model validation

It is difficult to validate the model using the study impoundments, as the model was parameterised with site-specific data, so a certain amount of agreement between model outputs and population status is expected. Nonetheless, there are some population parameters that can be used to gauge the model's accuracy. The asymptotic length (L_∞) of each population can reflect relative biomass density and growth rates (Lorenzen & Enberg, 2002), and it is expected that the relative modelled biomass densities in the study impoundments would be inversely proportional to their actual L_∞ values. However, the reverse is true. The model predicts Flat Rock to have the highest biomass density and Danjera the lowest (Table 7), but this is the same for their L_∞ values, with Flat Rock having by far the largest, albeit uncertain, L_∞ (Tables 1 & 2). Either the asymptotic length is a poor indicator of biomass density in these impoundments, or the model's estimates of population size, individual consumption or environmental production are inaccurate. Support for the accuracy of the model's estimate of population size is observed in the catch-per-unit-effort data (Table 7). Flat Rock did have the greatest relative biomass density (CPUE). The population L_∞ values therefore may be representing size-specific fishing pressure (Walters & Martell, 2004) rather than biomass density. Alternatively, the production in Flat Rock is greater than predicted, which may be the case given that proportion of autochthonous energy increases as impoundment size declines (Doi, 2009; Reynolds, 2008). This may not be sufficiently captured by the current model that focuses on autochthonous energy sources. The current model also uses the trophic-level estimates for the Brogo Dam population for all three sites. If the fish in Flat Rock feed generally from lower trophic levels than in Brogo Dam, then a greater biomass of fish could be supported from a given level of production. Site-specific stomach-content or stable isotope analyses would help refine this aspect of the model.

Further support for the model is gained from a mark–recapture experiment carried out in 2010 in Brogo Dam (Appendix S4). The estimated population size using numerous statistics (8530–10 560 fish) closely matches model simulations run for the same period (9147 fish; Table A4.1). Some agreement must be expected, as Brogo Dam was the impoundment used to estimate the mortality in the model (Appendix S1), but nonetheless it adds support to the model's accuracy.

Limitations and sources of error

The values used for the consumption parameters $b_{\max}$ and q were borrowed from other species, and the C_{av} model is a generic consumption model derived from many species (but not Australian bass). Species-specific data could improve the reliability of model outputs. If species-specific data are generally absent, the sensitivity analysis suggests that priority should be given to collecting data for trophic components (particularly the trophic level of the stocked fish) and mortality (M_r) and growth (L_∞). Trophic level has an inverse relationship with stocking density because the transfer of energy declines with increasing trophic level, meaning that populations at a higher trophic level are necessarily smaller for a given surplus productivity. An increase in the M_r parameter of the mortality function causes an increase in the density of fish that need to be stocked. L_∞ is inversely related to stocking density through both the growth and mortality components. An increase in L_∞ increases the body mass of the average Australian bass and also reduces the mortality rate, both of which increase the population's total consumption. This in turn decreases the density of fish that should be stocked. Given that L_∞ is such an influential parameter, and because it will change in response to biomass density (which is not expressed in the model), frequent stock analyses are recommended. The addition of a function that predicts the change in L_∞ in response to biomass density (e.g. Lorenzen & Enberg, 2002) could also benefit this model.

There is a question as to whether these fisheries are well designed for a predictive production-based model, given the large amount of variation that exists in the environment and in Australian bass (Smith *et al.*, 2011b,a). Therefore, there is a possibility that databases of stocking histories and stock assessments or yield-based regressions (Oglesby, 1977; Matuszek, 1978; Hanson & Leggett, 1982) are better suited to these environments. These approaches actually support a predictive production-based model, because chlorophyll-a can be correlated with fish yield (Downing & Plante, 1993; Leach *et al.*, 1987) and catch rates (Michaletz, 2009), although the relationship can be influenced by lake trophy (McQueen, Post & Mills, 1986). The 'maintain' stocking densities show much less uncertainty than the steady-state outputs because they do not incorporate the uncertainty associated with surplus production. These maintenance densities are therefore a robust alternative to the production-based estimates if the current state of the fishery is deemed suitable, and the available production is assumed reasonably constant.

The representation of carrying capacity in this model is a useful upper limit to stocking densities. Carrying capacity is often a target of stocking programmes (Li, 1999; Aprahamian *et al.*, 2003), but in the current model $C_{\min}$ is a scenario that should probably be avoided. The main limitation of using $C_{\min}$ to estimate carrying capacity is the assumption that the model components that determine surplus production (e.g. transfer efficiency, standing stock biomass) are independent of consumer pressure. This is unlikely to be true. It is unclear whether the carrying capacity in this model refers to the point of maximum population biomass (Daily & Ehrlich, 1992), and further research is needed to understand the relationship between consumption rates and carrying capacity.

There is no density-dependent mortality explicit in this model. This is because it could not be detected in the stocking histories of the study impoundments, despite some difference in the magnitude of stocking events. Density-dependent mortality is generally incorporated into population dynamic models through the stock–recruitment relationship (Hilborn & Walters, 1992), but because stocking can bypass the natural limitations which regulate wild populations in the long term (namely density-dependent recruitment), and because natural recruitment does not occur in these Australian bass fisheries (Harris, 1986), a stock–recruitment function was not used. Density-dependent mortality is indirectly considered in the model, however, because survivorship is negatively related to size (eqn 5). This means if populations experiencing density-dependent competition are correctly assigned lower L_∞ values, they are also assigned higher proportional mortality. Additionally, the $C_{\min}$ output addresses density-dependent mortality indirectly, because it represents the upper limit to population size and beyond this density-dependent mortality is considered to be absolute. The lack of an integrated component expressing density-dependent mortality means that the proportional survival is independent of stocking density, which could inflate the size of the actual population if there is a history of large stocking events. Thus, caution should be used if historical stocking densities exceed the estimated $C_{\min}$ steady-state stocking density.

There is also no compensatory growth explicit within the model. Growth rates are often density dependent (Lorenzen & Enberg, 2002; Post, Parkinson & Johnston, 1999; Walters & Juanes, 1993; Lorenzen, 1995), but are considered density independent in this model. Using various consumption scenarios does address the concept indirectly if consumption and growth rate are assumed to be positively related. The model outputs are, however, dependent on the growth rate estimated using the von Bertalanffy relationship. It is possible that incorporating density dependence in mortality and growth would improve the model's accuracy.

Estimating the available surplus production is associated with considerable uncertainty, and this resulted in steady-state stocking densities with wide probability distributions. Production is driven by the concentration of zooplankton and chlorophyll-a (for phytoplankton) in a stocked system. Temperature is the only parameter used to drive phytoplankton productivity (Appendix S2), but admittedly irradiance is equally important (Reynolds, 1984). A spatially explicit phytoplankton model that includes irradiance could benefit this stocking model. The demonstrated scenario using Australian bass used chlorophyll-a concentrations from 2010 only, and incorporating a time-series of data may be more realistic by incorporating interannual variation in phytoplankton productivity.

In conclusion, this study shows that a general production-based stocking model can be a useful management aid for stocked fisheries, particularly by acknowledging differing management objectives in the model's consumption component. The model demonstrates that there may not be a single 'optimal' stocking density for a specific impoundment, owing to the necessary trade-off between the consumption rates (akin to growth rates) of individuals and a stocked population's size. Seasonal variation in both consumption rates and prey production influences stocking density, and further research is needed to determine whether it is the seasonal minima or maxima in prey production, which is a better indicator of a population's size. A precautionary stance would suggest that, for a given consumption scenario, the stocking densities are based on the seasonal minima. It was also observed that bottlenecks may not always be in winter, as Flat Rock Dam showed higher relative consumption in winter than in summer. This supports a site-specific approach to stocking management.

The steady-state basis for providing stocking density estimates should also encourage sustainable stocking practices in closed fisheries. This requires significant investment in the forecasting of stocking densities, but a stocking regime that focuses on approaching a steady-state fishery is the one most likely to meet its objectives. It may not always be possible for managers to regularly stock fish at ecologically sustainable densities, owing to economic or practical limitations, but it should be a priority. Like all stocking models, this model would be most beneficial when used in conjunction with other assessment tools as part of a comprehensive programme (Taylor *et al.*, 2005; Molony *et al.*, 2003) to ensure that stocked populations are managed effectively.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Mortality.

Appendix S2. Production.

Appendix S3. Trophic level and diet composition.

Appendix S4. Mark–recapture and CPUE.

Appendix S5. Stocking histories.

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